

What exactly is *Antheraea paphia* (LINNAEUS, 1758)?

(Lepidoptera, Saturniidae)

by

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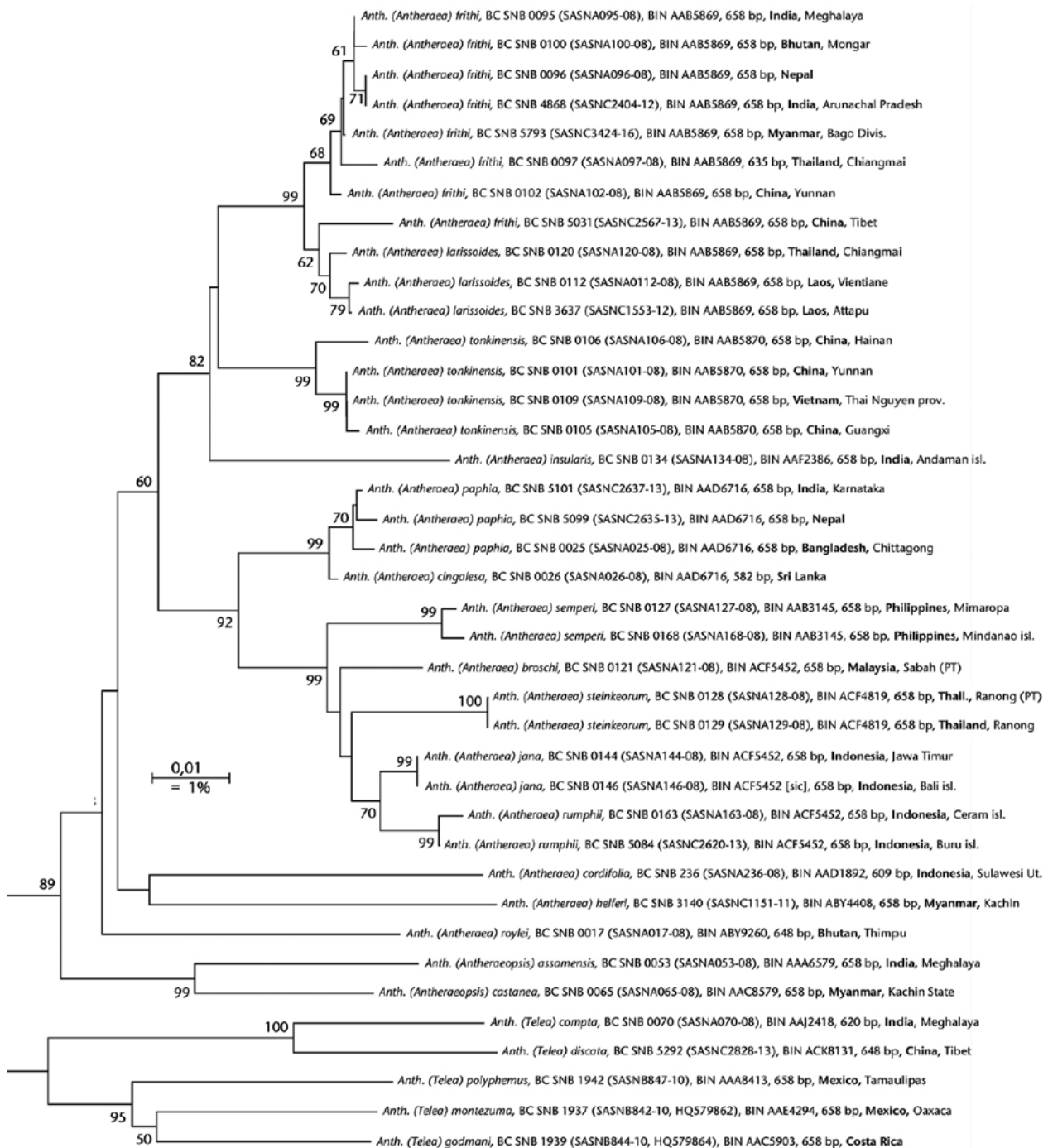
Abstract: For more than 200 years there has been considerable confusion pertaining to the correct application of the names *Antheraea paphia* (LINNAEUS, 1758) and *Antheraea mylitta* (DRURY, 1773), with many authors historically and today using one or the other or both names for the tasar silkmoth in India and neighboring countries. Arguments are presented that the two names are synonyms, and that only the earlier published name *A. paphia* (L.) should be used. Some notes on the history of the misleading interpretations of the type material of *A. paphia* (L.) and possible taxonomic solutions are presented. There is also disagreement about the correct taxonomic treatment of the entities named *A. paphia* (L.) and *A. cingalesa* MOORE, 1883. One hypothesis is that *A. paphia* (L.) from India and *A. cingalesa* MOORE from Sri Lanka were both derived thousands of years ago through selective breeding by humans for their silk from the progenitor *A. frithi* MOORE, 1859 in the Himalayan region. The other hypothesis is that the names *A. paphia* (L.), *A. cingalesa* MOORE, and *A. frithi* MOORE refer to three distinct and naturally occurring species that evolved without human interference. Detailed arguments to support these opposing hypotheses are presented.

Zusammenfassung: Mehr als 200 Jahre gab es Ungewißheit zur richtigen Verwendung der Namen *Antheraea paphia* (LINNAEUS, 1758) und *Antheraea mylitta* (DRURY, 1773), so daß viele Autoren in historischen und aktuellen Publikationen entweder den einen oder den anderen Namen, in manchen Fällen auch beide simultan, für den “Tasar Silkmoth” aus Indien und benachbarten Ländern gebrauchten. Es werden Argumente aufgeführt, die aufzeigen, daß beide Taxa Synonyme zueinander sind und daher der zuerst publizierte Name *A. paphia* (L.) anzuwenden ist. Eine Übersicht über die Geschichte verschiedener Interpretationen des Typenmaterials von *A. paphia* (L.) und sich daraus ergebender taxonomischer Folgen werden aufgezeigt. In der Literatur gibt es auch Unklarheit über die richtige taxonomische Stellung der Taxa *A. paphia* (L.) und *A. cingalesa* MOORE: Eine Hypothese ist, daß sowohl die indische *A. paphia* (L.) als auch die srilankesische *A. cingalesa* MOORE durch selektives Herauszüchten zur Seidenherstellung vom Menschen aus ihrem wild vorkommenden Vorfahren *A. frithi* MOORE, 1859 aus der Himalaya-Region entstanden sind. Eine andere Hypothese ist, daß sich alle drei Namen *A. paphia* (L.), *A. cingalesa* MOORE und *A. frithi* MOORE auf drei verschiedene und in der Natur vorkommende Taxa beziehen. In der vorliegenden Arbeit werden die beiden sich entgegenstehenden Hypothesen vorgestellt.

Introduction: The tasar silkmoth, *Antheraea paphia* (L.), is of considerable economic importance in modern India, and its silk has important cultural significance with the Indian public. It ranges primarily in the eastern edge of the Deccan Plateau and in the Eastern Ghats, from West Bengal to Andhra Pradesh, where its cocoons are collected by humans to be processed into textiles. Tasar sericulture provides income and employment to many people in India, and such pieces are always handwoven. Even today, garments made from tasar silk are frequently worn as saris by brides and as kurtas by grooms, and uncut cloth like saris, scarves, and dupattas composed of tasar silk are highly popular all across India. Some nice samples were figured recently by TRAVIS & PEIGLER (2016), and also here in this work four handwoven shawls made from tasar silk are shown (figs. 79, 80). Consequently, the Central Silk Board, a federal agency in India, actively promotes the production and marketing of this type of wild silk, which is also spelled tassar and tussar (JOLLY et al., 1974; SINHA et al., 2006; KAVANE & SATHE, 2011; ZETHNER et al., 2012).

There has been confusion for the past 243 years as to which scientific name should be applied to the tasar silkmoth, and inconsistent usage of the names *A. paphia* (L.) and *A. mylitta* (DRURY) can still be seen in the taxonomic and sericultural literature that is published in India even today. In this report we will present evidence that the two names are synonyms, and we will discuss whether the tasar silkmoth is a true species (a naturally occurring insect), or if it was possibly derived millennia ago from the Himalayan species *A. frithi* MOORE. We also address the same question for the closely related *A. cingalesa* MOORE, 1883, described from Sri Lanka.

We have elected to restrict this study to the moths that fly in India, Nepal, Bhutan, southern China (Tibet and Yunnan Provinces), Myanmar, and Sri Lanka, although there are populations of *A. frithi* MOORE farther east on the Asian mainland that may be conspecific with those in India. Even as far east as on some Indonesian or Philippine islands there occur some taxa which resemble, especially in ♀♀, these on which we report here, but those are definitely not conspecific with any Indian *Antheraea*. For example, *A. rumphii* (C. FEFDER, 1861) in eastern Indonesia superficially looks like *A. paphia* (L.) from India, and some of its synonyms were even described or cited as subspecies of *A. paphia* (L.) by BOUVIER (1928, 1930, 1936). Related species that look similar to *A. frithi* MOORE occur in the whole subtropical and tropical parts of Southeast Asia, some of which are included for comparison in our figure showing results of DNA analysis with the Mega5 neighbour joining tree (text figure 1).



Text figure 1: NJ-barcode-tree ex Mega5: selected *Antheraea* records ex collection S. NAUMANN [mainly *A. frithi* MOORE, 1859 and *A. paphia* (LINNAEUS, 1758)], outgroups *Antheraeopsis*, *Telea* and some others (*cordifolia*, *roylei*, *helferi*) shown (kindly produced by W. A. NÄSSIG).

The identity of *Antheraea paphia* (LINNAEUS, 1758)

Up to now the treatment of the name *paphia* has been somewhat uncertain in the literature, due to the fact that type specimens of LINNAEUS are, as often is the case, no longer available to science, either because he referred in his descriptions only to figures in earlier publications, or that material formerly in his hands was destroyed and replaced by other specimens, held today in the collections of Museum in Uppsala or the Linnean Society in London. In the case of *Phalaena Bombyx Paphia*, LINNAEUS (1758: 496) referred in his description to figures of two species which clearly belong to different taxa, and he had specimen(s) of a third species personally in his hands. This conglomerate consists of following:

1. Specimen or specimens of unknown sex and identity in Museum Ludovicae Ulricaе (Uppsala).
2. A figure in PETIVER (1702: pl. 29) showing a ♂ of *Nudaurelia dione* (FABRICIUS, 1793) or nearly related (mentioned as *Phalaena guineensis*), originating from the Guinea coast, West Africa.
3. A figure in CATESBY (1743, pl. 91) showing a ♂ of *Antheraea (Telea) polyphemus* CRAMER, 1776 [cited as *Phalaena ingens*] from Carolina, USA.

AURIVILLIUS (1882: 148) was aware of this situation, and wrote that LINNAEUS deposited the “wings with ocelli of both specimens” (translation from Latin text by J. LUX) in Museo Ludovicae Ulricaе. It remains unclear if LINNAEUS presented only loose wings to the museum collection, and if those were later replaced by a complete specimen (or specimens), or if this is just some unfortunate wording by AURIVILLIUS. Nevertheless, he showed in his fig. 2 a ♂ with legend “*Antheraea paphia* (L.), secundum specimen typicum”, and this specimen is still preserved in the collections of Museum of Evolution, Uppsala. It remains unclear what the second specimen could have been. We figure here this specimen from dorsal and ventral side (figs. 1, 2; photo credit: H. MEJLON). This is the only preserved possible type specimen of the name *paphia*; there are no further type specimens in Uppsala, nor are there any in the Linnean Society collection in London or elsewhere, e.g. in the natural history museum collections of Stockholm, Copenhagen, or the Natural History Museum, London. The specimen was mentioned in the type catalogue of the museum in Uppsala (WALLIN, 2001: 39) with no. #2007 already. A pair of *A. paphia* (L.) in the collection of LINNAEUS at the Linnean Society of London was examined by PEIGLER in 1995, but these specimens were added after James Edward SMITH purchased the collection.

As already mentioned by AURIVILLIUS (1882: 148), it would not make much sense under the ideal of perfect taxonomy to attribute the name *paphia* to African or North American insects that are well-known and widely accepted under the names *dione* and *polyphemus*, respectively; and also by the situation that those two species were merely cited from figures in literature in LINNAEUS' work, yet there still exists another real specimen with potential type status, so it becomes clear that the name *paphia* should refer to an Asian insect. However, closer examination of the specimen in Uppsala reveals that this is not the species widely accepted to be *A. paphia* (L.) nowadays, but a different species with uncertain identity. It shows similarities with the Moluccan taxon *A. rumphii* (C. FEFDER) (mentioned as “*Amboinensis*” by AURIVILLIUS), and AURIVILLIUS found similarities with *A. celebensis* WATSON, 1915 from Sulawesi; LINNAEUS (1767: 809) himself, in a later edition of his work, mentioned aside from the works of PETIVER and CATESBY in a footnote “*Rumph.*”, referring to Moluccan specimens. This could also explain why BOUVIER (1928, 1930) and D'ABRERA (2012: 128-133) considered some Moluccan *Antheraea* to be subspecies of *A. paphia* (L.).

FABRICIUS, one of the students of LINNAEUS, published some entomological catalogues and was probably the first author who referred to *A. paphia* (L.) as solely an Asian species. In three of his publications (1774, 1781, 1793), he referred to *A. paphia* (L.) the publications of LINNAEUS, PETIVER [sic], and RUMPHIUS, with “habitat in Asia”, and to *A. mylitta* (DRURY) by DRURY, CRAMER, and SEBA, with “habitat Indiae orientalis”; the citation of PETIVER under *A. paphia* (L.) is probably a lapsus, but the rest of this classification makes clear that FABRICIUS knew of the still extant type material of LINNAEUS. In the last publication (1793: 410) he even described the taxon *Bombyx dione* from Guinea coast which makes clear that the specimen figured by PETIVER was clearly not the taxon which LINNAEUS wanted to describe, judging from LINNAEUS' material. A further detail is that we have determined that the specimen figured by SEBA (1765: pl. 24, fig. 5, 6) is also not *A. paphia* (L.), but most probably a ♂ of *A. helferi* MOORE, 1858.

Finally, CRAMER (1779) referred with *A. paphia* (L.) only to Asian species and figured all nicely (pl. CXLVI: reddish brown ♀; CXLVII: yellow ♀♀; CXLVIII: reddish brown ♂), and he mentioned *A. mylitta* (DRURY) to be the same species. For his specimens he gave localities as Coromandel coast (which is the southeastern Indian coast south of the Eastern Ghats), Bengalen, Tranquebar (in Tamil Nadu coast) and Amboina (Ambon Island, Moluccas, Indonesia). However, KIRBY (1892: 757) again attributed *A. paphia* (L.) to an African species, but considered *A. mylitta* (DRURY) to be of Asian origin.

As shown with the literature review above, we now have a situation for *A. paphia* (L.) where a name is based on three different species originating from three different continents, and the only existing potential type is a ♂ without locality data and a damaged abdomen within a genus consisting of many very similar taxa where even a genitalic dissection sometimes provides no reliable specific identification. The Code (ICZN 1999) gives support to solve such unsatisfactory cases: Recommendation 73B says that there is some preference for specimens studied to those known only from descriptions and figures in literature, so it is clear that the extant specimen should have priority over just cited figures. Article 75.5. regulates the replacement of unidentifiable name-bearing types by a neotype, which would make sense for a specimen like the one we found in Uppsala, by the reasons mentioned above; in addition to this fact, Article 75.6.

regulates the conservation of prevailing usage of names by a neotype. The name *paphia* was used for long time in almost all cases of older and modern literature for the Indian taxon which produces tasar silk, but not for a Moluccan or other East Asian *Antheraea* taxon. Due to this situation, we will, after publication of this, submit an official case to the Commission for Zoological Nomenclature, to rule about the rejection of the only existant type of *A. paphia* (L.), and to replace that by a neotype specimen with precise locality from southeastern India, in order to fix the name *paphia* and give stability to zoological nomenclature. By that action, the synonymy of *A. paphia* (L.) with *A. mylitta* (DRURY) should become clear as well, although DRURY's type specimens are also of somewhat dubious status (compare handling of DRURY types in PEIGLER & NAUMANN, 2003: 76). At least the origin of such a specimen will be certain, and thus its identification.

The synonymy of the names *Antheraea paphia* (LINNAEUS, 1758) and *A. mylitta* (DRURY, 1773)

Antheraea paphia (L.) was described by LINNAEUS (1758: 496) as *Phalaena Bombyx Paphia*, and *A. mylitta* (DRURY) was named by DRURY (1773: 8) as *Phalaena Attacus Mylitta* (fig. 35: ♂ figured by DRURY). Several authors, even as early as ROXBURGH (1804), considered the two names to be synonyms, whereas others (KIRBY, 1892; BOUVIER, 1936) treated them as separate species, but BOUVIER was generally reluctant to synonymize any names in his extensive writings on Saturniidae. Still others (e.g., SEITZ, 1928: 509; SCHÜSSLER, 1933: 183) classified *A. mylitta* (DRURY) as a subspecies of *A. paphia* (L.). Both names were listed as separate species by HÜBNER (1819: 152) in his original description of the genus *Antheraea*. WARDLE (1879, 1881), COTES & SWINHOLE (1887), SONTONNAX (1899), QUAJAT (1904) and CLARY (2009) treated the two names as synonyms, but considered *A. mylitta* (DRURY) to be the correct one, although *A. paphia* (L.) is the older name. The catalogue of SCHÜSSLER provides a full account of the nomenclatural history of both names up until 1933, vis-à-vis, how hundreds of authors treated these names. In their taxonomic treatise of Indian saturniids, ARORA & GUPTA (1979) used the name *A. paphia* (L.) for this moth, and cited *A. mylitta* (DRURY) as a junior synonym, as did WATT (1893) and PEIGLER & WANG (1996). LAMPE (2010) and VENKATARAMAN (2010) called it *A. paphia* (L.), and did not mention *A. mylitta* (DRURY). Although *A. paphia* (L.) is variable, we agree with ARORA & GUPTA that this variability can all be reconciled under a single species. VILLIARD (1969) reared both entities from eggs that he purchased from livestock dealers, but lamented that he could not really distinguish between the two.

The names *A. paphia* (L.) and *A. mylitta* (DRURY) are both commonly used today in the sericultural literature published in India. MILLER & NAYAK (1998) acknowledged that some authors consider the two names to be synonyms, but stated that both names should be maintained. They argued that “considerably more body weight is allocated to eggs in *A. paphia* (L.) than in *A. mylitta* (DRURY),” and that *A. mylitta* (DRURY) is semi-domesticated and has a narrower altitudinal range as compared to the wild *A. paphia* (L.), which “establishes itself naturally.” DEY et al. (2004) concurred that *A. paphia* (L.) “is completely wild” but *A. mylitta* (DRURY) is “semi-domesticated.” Then DEY et al. (2008) stated explicitly that the names were synonyms by writing “Tropical tasar silk is produced by the tasar silk moth *Antheraea paphia* LINN. (= *Antheraea mylitta* DRURY)...” in their paper. On the contrary, PANDIT et al. (2014) considered the name *A. mylitta* (DRURY) to refer to the wild form. Lastly, YADAV (2013) considered the form in the Vidarbha Forest of the Bhandara District of eastern Maharashtra to be *A. paphia* (L.), whereas WAZALWAR et al. (2013) considered *A. mylitta* (DRURY) to be the correct name for that population in the same forest. All six papers cited in this paragraph were published in the same journal, and the last two papers appeared in the same issue. We believe that such inconsistent usage of the two names by Indian authors actually lends support that they should be treated as synonyms, and only *A. paphia* (L.) should be used. In any case, numerous so-called ecoraces have been named, some dating back more than a century (MUKERJI, 1903: 106); some of these names are assigned to *A. mylitta* (DRURY) and others to *A. paphia* (L.). MOORE (1892) named several more taxa that are now considered to be synonyms of *A. paphia* (L.). Moreover, KAVANE & SATHE (2011) named nine new “subspecies” of *A. mylitta* (DRURY), but these were all formally synonymized by PAUKSTADT & PAUKSTADT (2013), and we concur that those names do not represent valid subspecies. JOLLY (1981) wrote that the ecoraces of *A. mylitta* (DRURY) “show remarkable degree of differentiation in appearance and are often mistaken for different species.” It is obvious that the two names have been confused going back to the 1700s, and much of this confusion persists today among sericulturists, but not by taxonomists who study Saturniidae. *Antheraea paphia* (L.) is a variable insect, but we believe that the name *A. mylitta* (DRURY) is a junior subjective synonym.

The relationship between *Antheraea paphia* (LINNAEUS, 1758), *A. cingalesa* MOORE, 1883, and *A. frithi* MOORE, 1859

Although both authors are in full agreement pertaining to the synonymy and taxonomy of the names *A. paphia* (L.) and *A. mylitta* (DRURY), we do not have the same interpretation of what the names *A. paphia* (L.) and *A. cingalesa* MOORE represent. The first author believes that *A. paphia* (L.) and *A. cingalesa* MOORE have resulted from artificial selection and range extension by humans in India and Sri Lanka for the past two or three thousand years, derived from the progenitor *A. frithi* MOORE. The second author believes that *A. paphia* (L.) and *A. cingalesa* MOORE are valid species that evolved without human interference, and are thus distinct from the separate species *A. frithi* MOORE. We present our arguments below in separate subsections.

Evidence for the hypothesis that *Antheraea frithi* MOORE, 1859 is the progenitor of *A. paphia* (LINNAEUS, 1758) and *A. cingalesa* MOORE, 1883

WARDLE (1881) opined that “there is but little doubt that this silk [tassar] has been utilized for many centuries in India” and he provided an exhaustive account of tasar sericulture, and so did WATT (1893: 1002-1009) and MUKERJI (1903: 103-138). GOOD et al. (2009) critically analyzed silk samples from archaeological sites around Harappa, in present-day Punjab Province, Pakistan, and reported that reeled silk samples from sites dating back to about 2450 BC matched those of *A. paphia* (L.) and *A. assamensis* (HELPER, 1837), the latter being the source of muga silk in Assam. These archaeological data provide direct evidence that silks from *Antheraea* have been exploited by humans in the Himalayan region for more than 4000 years. There is a consensus among scholars that *Bombyx mori* (L.) has been exploited for silk for at least 5000 years, and *Antheraea pernyi* (GUÉRIN-MÉNEVILLE, 1855) has been used in China for at least 3000 years, according to Chinese references cited by PEIGLER (2012). Sericulture based on *Samia ricini* (WM. JONES, 1791) probably dates back at least two millennia (PEIGLER & NAUMANN, 2003).

The four primary sources of silk in the world today (and historically) are therefore, not surprisingly, *B. mori* (L.), *A. pernyi* (GUÉRIN-MÉNEVILLE), *S. ricini* (WM. JONES), and *A. paphia* (L.). Of these, *B. mori* (L.) and *S. ricini* (WM. JONES) exist only in captivity, and their progenitors are known to be *B. mandarina* (MOORE, 1872) and *Samia canningi* (HUTTON, 1859), the latter supported by diverse data (genitalia, chromosome numbers, etc.) cited by PEIGLER & NAUMANN (2003). In a sense, *A. pernyi* (GUÉRIN-MÉNEVILLE) exists primarily in captivity, because mature larvae are brought indoors where cocoons are formed, matings occur, and the resulting eggs placed back out into fields of pruned oaks. This sort of husbandry of placing eggs and larvae on trees and then collecting the resulting cocoons is very similar to what happens with *A. paphia* (L.) in many areas of India (ZETHNER et al., 2012). If these methods of facilitated rearing have been used in India for centuries or even millennia to obtain tasar silk, many opportunities for range extension and artificial selection would have been consistently available.

These four species that are mass reared indoors or enhanced and protected outdoors share critical traits, the main one being an exceptionally large cocoon, or in the case of *A. pernyi* (GUÉRIN-MÉNEVILLE), a normal-sized cocoon containing far more silk than any other species of *Antheraea*. The peduncles have been lost completely in *B. mori* (L.) and *S. ricini* (WM. JONES), and are greatly reduced and often absent in *A. pernyi* (GUÉRIN-MÉNEVILLE). Since *A. paphia* (L.) is reared outdoors and cocoons are formed before being harvested, the peduncle would not be lost by artificial selection (cocoon fig. 55). All four of the primary silk producers have numerous named purebred lines, variously called ecoraces, strains, or varieties (QUAJAT, 1904; SINHA et al., 2006), which can be used as an argument to support the hypothesis that the tasar silkmoth [*A. paphia* (L.)] is indeed of sericultural origin.

PEIGLER (2012) and PEIGLER & CHUTIA (2013) proposed that *A. pernyi* (GUÉRIN-MÉNEVILLE) was mass reared and artificially selected in regions of central and northeastern China that are farther north than wild populations of the presumed progenitor, which is the Himalayan *A. roylei* MOORE, 1858, because this would have prevented the gene pools of the cultivated stocks (that were being selectively improved) from being polluted by wild moths. If *A. frithi* MOORE is indeed the progenitor of *A. paphia* (L.), that artificial selection would have occurred in the Deccan Plateau and/or Eastern Ghats, south of the Himalayan distribution of *A. frithi* MOORE. This factor may account for why tasar silk is not cultivated in the Himalayas beyond lower elevations of West Bengal, even in places of Northeast India where other wild silkmoths are maximally exploited, i.e., muga, eri, and tussah (=oak tasar). In any case, tasar sericulture flourishes mainly in Jharkhand, Chhattisgarh, and Odisha-areas where *A. frithi* MOORE does not occur. PEIGLER & WANG (1996) published colour photographs of adults and cocoons of the Godamodal and Sukinda ecoraces from Odisha.

To expand on the aforementioned point, the geographical distributions of *A. paphia* (L.) and *A. frithi* MOORE in India are defined and separated by altitude. Although DEVI et al. (2011: table 1) cited tasar culture [*A. paphia* (L.)] in the village of Jiribam, Manipur, the other literature such as JOLLY (1981), SINHA et al. (2006, maps 8, 9), and GOGOI et al. (2014) leave no doubt that tasar culture is quite absent in the Northeast of India. As mentioned above, tasar culture in West Bengal is limited to the western areas (SINHA et al., map 5) that have the lowest elevations. Attempts in ancient times to select artificially for larger cocoons in *A. paphia* (L.) in the areas where *A. frithi* MOORE flies would have been unsuccessful, because tasar culture is primarily an outdoor activity. The cocoons of *A. frithi* MOORE are less than half the size of cocoons of *A. paphia* (L.) (CHUTIA et al., 2014: table 2). There is no apparent ecological reason why the cocoons of *A. paphia* (L.) should be so huge, and the same point applies to the very large cocoons of *S. ricini* (WM. JONES) and *B. mori* (L.). Except for those of the gigantic Attacini (*Attacus*, *Coscinocera*, *Archaeoattacus*) and *Argema mittrei* (GUÉRIN-MÉNEVILLE, 1847), the cocoons of *A. paphia* (L.) are the largest in the family Saturniidae.

RONDOT (1887: 176-177) quoted LIOTARD for saying that *A. frithi* MOORE was one of the three main species for tussah [tassar] silk. QUAJAT (1904: 45) included *A. frithi* MOORE among the important *Antheraea* silk producers in his monograph, and stated that its cocoons contain a lot of silk. The scientists and sericulturists in India who work with wild silks, now called vanya silks in India, are beginning to be aware that *A. frithi* MOORE is not just another wild species of *Antheraea*. For example, in the preamble to their comprehensive book, SINHA et al. (2006: viii) wrote that “cultivation of 21 species of tree species on which vanya silkworms of Tassar, Oak Tassar, Muga, Eri, and *A. frithi* MOORE could be reared by tribals and non-tribals...”. *Antheraea frithi* MOORE was referred to as “the wild tasar silkmoth” by CHUTIA et al. (2014). There is an increasing recognition that the cocoon of *A. frithi* MOORE contains ample silk that can be processed like tasar in areas where enough of its cocoons can be collected. These points all suggest that cocoons of

A. frithi MOORE would have been viewed as a good source of silk by peoples in ancient India, and husbandry with its associated intentional or unintentional artificial selection followed as a consequence. In his review of *Antheraea*, D'ABRERA (2012: 128-131, 140-141) accepted PEIGLER's arguments that the entities known under the names *A. pernyi* (GUÉRIN-MÉNEVILLE) and *A. paphia* (L.) actually resulted from millennia of artificial selection.

The primary foodplants of *A. frithi* MOORE are stated to be *Shorea robusta* (Dipterocarpaceae) and *Terminalia arjuna* (Combretaceae) (CHUTIA et al., 2014), and these two trees are consistently reported to be the main ones used in tasar culture of *A. paphia* (L.) as well (JOLLY et al., 1974; ARORA & GUPTA, 1979; SINHA et al., 2006; CLARY, 2009; KAVANE & SATHE, 2011; ZETHNER et al., 2012). Both insects feed on several other species of trees, approaching being polyphagous. Until the present work, the only published drawings comparing ♂ genitalia of *A. paphia* (L.) and *A. frithi* MOORE were given by ARORA & GUPTA (1979). Although differences can be seen between the genitalia in our figures here, the two appear to be basically the same overall, especially when compared to those of other species in the genus in the same work. The larval stages of *A. paphia* (L.) and *A. frithi* MOORE also appear to be the same when compared to those of other *Antheraea* (LAMPE, 2010: pls. 270, 275). More importantly, the size, arrangement, and structure of the setae on the scoli are virtually identical, except for the dorsal scoli on the 9th abdominal segment, as shown in the pictorial chart of JOLLY (1981) and JOLLY et al. (1974). These latter authors also gave diagrams and descriptions showing that the egg structure and follicular imprints can be interpreted as being the same in both species, but different from those of other *Antheraea*. ♂♂ of both species have the same dark brown or orangish colour forms for the ground colour, although ♀♀ of *A. paphia* (L.) have more variation in ground colour (grey, beige, yellow, orangish) than the usually yellow or beige ♀♀ of *A. frithi* MOORE (see LAMPE, 2010: 276). As for wing pattern, it appears that the undulating lines seen in *A. frithi* MOORE have been lost or greatly reduced in *A. paphia* (L.), but the discal spots became larger. When taken collectively, all of these morphological characters provide strong evidence that *A. paphia* (L.) and *A. frithi* MOORE are the same species biologically, or are each other's nearest relatives if they are not the same species. When comparing egg chorions, larvae, wing pattern, and genitalia, it can be argued that the two entities are much more alike than different.

COTES & SWINHOE (1889: 228) treated *A. cingalesa* MOORE from Sri Lanka as a full species, but later COTES (1891-1893: 80) doubted that it was distinct. ROTHSCHILD (1895) listed it as an aberration of *A. mylitta* (DRURY). SCHÜSSLER (1933: 182) treated *A. cingalesa* MOORE as a subspecies of *A. paphia* (L.), BOUVIER (1936: 162) and JOLLY (1981) considered it to be a synonym of *A. mylitta* (DRURY), and ARORA & GUPTA (1979) cited *A. cingalesa* MOORE as a synonym of *A. paphia* (L.). There are no consistent traits in the wing patterns and genitalia to separate *A. cingalesa* MOORE from populations in India. Therefore, *A. cingalesa* MOORE is probably a synonym of *A. paphia* (L.). If true, this would suggest that humans transported cultures of the tasar silkworm from India to Sri Lanka. Humans have engaged in active trade between the Sri Lanka and the mainland (India) for at least 2500 years, so introduction of the tasar silkworms from India to Sri Lanka would not be expected to be documented in literature. ALUTHWATTHA (2013) treated *A. cingalesa* MOORE as a full species, but the barcode data he presented actually indicate that *A. paphia* (L.) and *A. cingalesa* MOORE are conspecific. No authors appear to have presented any diagnostic characters to separate moths of *A. paphia* (L.) from *A. cingalesa* MOORE, probably because there are not any differences. Moths collected in Sri Lanka fall within the variation of *A. paphia* (L.). Based on the barcode results shown here in text figure 1, we see one further possibility, which would be that *A. frithi* MOORE and *A. paphia* (L.) are separate species that evolved naturally, but *A. cingalesa* MOORE was derived through artificial selection and transported from India to Sri Lanka by humans in ancient times.

Evidence for the hypothesis that all three names represent separate and natural species

Antheraea frithi MOORE is a species occurring in the sub-Himalayan areas of mainland Asia in low to medium altitudes up to 2200 m. Records exist for northeastern India (e.g., MOORE, 1862; COTES, 1891-1893; COTES & SWINHOE, [1889]; WATSON, 1911; ARORA & GUPTA, 1979; GURULE & NIKAM, 2013), Nepal (e.g. ALLEN, 1993, cited as *A. frithi frithi*), Bhutan, northern and central Myanmar, China (Tibet and western Yunnan), and northern Thailand (records in junior author's collection). We figure some ♂♂ and ♀♀ specimens from all over the distribution (figs. 21-34) plus ♂ genitalia structures (figs. 44-46). The species is characterized in the ♂♂ by its brownish orange colour with undulate markings and large, almost rounded eyespots with hyaline center; the ♀♀ always are of a dull yellow colour, without or with minimal undulate markings, relatively large ocellus with huge inner hyaline center. The Bhutanese population was reared successfully on *Quercus* in Germany in 2007, and the complete life circle is figured here (figs. 68-77). In northeastern India, State of Manipur, it was reared on *Terminalia arjuna*, and the preimaginals recorded and shown by CHUTIA et al. (2014), who also listed wild foodplants of *A. frithi* MOORE in Assam. Cocoons are relatively small, with a small, loose peduncle spun along the petiole of the leave in which the cocoon is spun (figs. 77, 78, and in CHUTIA et al., 2014), as is seen in several other species of *Antheraea*. Amongst nearest relatives of *A. frithi* MOORE are e.g. *A. larissoides* BOUVIER, 1928 from Thailand and Laos, *A. tonkinensis* BOUVIER, 1936 from Vietnam and southern China, and *A. insularis* WATSON, 1914 from the Andaman Islands, plus some others. These species are also included with their barcoding results in the figured neighbor joining tree (text fig. 1).

In contrast to *A. frithi* MOORE, *A. paphia* (L.) occurs in lower elevations all over the Indian subcontinent, plus in adjacent lowland areas of Nepal and Bangladesh. No records exist for that species for the sub-Himalayan slopes or higher elevations in Northeast India to the border with Myanmar, or farther east. As mentioned by various earlier authors (e.g., WAILLY, 1881; WATSON, 1911; SCHÜSSLER, 1937), the species is reared in semi-captivity for tasar silk in India. Eggs

or young larvae are set free in plantations, and resulting cocoons are harvested later for their silk, and also cocoons are collected from the wild and brought to the silk factories (HELPER, 1837; MOORE, 1862). By this it should be clear that there exist populations of this moth in the wild and simultaneously in semi-captivity on farms, from where also individuals may escape back to the wild again. Therefore, Western collections often contain captive-bred specimens, but there exist also series of wild collected specimens from forested areas in Nepal or southern India.

Specimens of *A. paphia* (L.) are generally larger than those of *A. frithi* MOORE, have larger wing ocelli, and show more variability in colour. ♂♂ have a more elongate forewing apex, in contrast to the yellowish orange males of *A. frithi* MOORE there occur ochreous, orange, reddish and chestnut brown varieties, all almost without the undulate lines on the wings and with an almost straight postmedian line. Antennae are longer and have longer rami. The ♂ genitalia structures of *A. paphia* (L.) (figs. 36-39) are generally larger, the uncus is longer, the ventral process of the valves much broader, the dorsal process as well, with a knob-like dorsal projection, and the setae are more stable and therefore shorter. The labides are higher, with a knob-like process. In larger series of genitalia preparations for the genus *Antheraea*, subgenus *Antheraea* (see NÄSSIG, 1991), it becomes obvious that these are significant differences which clearly show that both taxa represent separate species. ♀♀ occur in yellow, grey, ochreous and greyish brown forms, and have very large transparent parts of their wing ocelli. ♂ and ♀ samples from different places in India plus Bangladesh and Nepal are figured for comparison (figs. 3-16). JOLLY (1981) figured follicular imprints of the eggs of different *Antheraea* species, and showed clear differences in the structures between those of *A. frithi* MOORE and *A. paphia* (L.). The species was reared on *Quercus* in Germany, and we figure different larval instars plus the ovoid large cocoons with the typical long peduncle, cut from the branches of their food trees, and living adults (figs. 47-56). The preimaginals were also nicely figured by LAMPE (2010), and also here differences to those of *A. frithi* MOORE become obvious in detail: First instar larvae are of more greenish colour with less intense intersegmental stripes; third instar larvae have lateral blue tubercles and black dorsal ones on second and third thoracic segments (compare also to figures in CHUTIA et al., 2014), and dorsal setae in fourth and last instar are slightly different. However, the main difference is in the cocoon, which is ovoid, large with long peduncle in *A. paphia* (L.) and smaller, elongate, sometimes covered with yellow pigments, and has a tiny peduncle in *A. frithi* MOORE. CHEN et al. (2012) showed also the different micro-structures of cocoons of *A. paphia* (L.) and *A. frithi* MOORE.

For different Indian populations of *A. paphia* (L.) several taxa were described (overview for older taxa in PAUKSTADT et al., 2000; also PAUKSTADT & PAUKSTADT, 2013) all of which are synonyms of *A. paphia* (L.). As stated above, several eco-races, strains, or varieties (QUAJAT, 1904; SINHA et al., 2006) were named, similar to other cases of silk-producing moths, but those refer only to the cultivated part of *A. paphia* (L.) and not to its wild populations, thereby this is no argument that *A. paphia* (L.) is entirely man-made and of sericultural origin. A similar hypothesis, that *A. roylei* MOORE is the wild progenitor of the mass-reared oak silkmoth *A. pernyi* (GUÉRIN-MÉNEVILLE), was proposed by PEIGLER (2012) and PEIGLER & CHUTIA (2013). NAUMANN and NÄSSIG, (2015) argued extensively against this hypothesis in their comments, and stated that both *A. roylei* MOORE and *A. pernyi* (GUÉRIN-MÉNEVILLE) are natural species, with some more relatives occurring in Asia that were not considered by the proposing authors. JOLLY et al. (1973, 1981) reported that artificial hybrids between *A. frithi* MOORE and *A. paphia* (L.) were sterile in first generation, a result that supports the status of separate species.

The nearest relative to *A. paphia* (L.) is *A. cingalesa* MOORE on Sri Lanka. The population of this insular taxon is well separated from mainland India, and as in other saturniids from Sri Lanka, is endemic. There is no evidence from literature that the *Antheraea* population in Sri Lanka was introduced by man for sericulture, and again compared with other saturniid genera, it is more plausible that there was a naturally-occurring representative of each genus with its nearly related counterpart on the southern Indian subcontinent - but not all genera reached the island. ♂ specimens of *A. cingalesa* MOORE are evidently smaller than those of *A. paphia* (L.), have smaller hyaline parts of the ocelli; there occur reddish and brownish samples. ♂ genitalia structures differ from those of *A. paphia* (L.) by their smaller size overall and correspondingly smaller size of the “dorsal hook” (NÄSSIG, 1991) of the 8th abdominal segment (compare figs. 40-43). ♀♀ are slightly smaller than those of *A. paphia* (L.), and have less huge wing ocelli. There probably exist the same colour forms. We figure some specimens to show the variability of this taxon (figs. 17-20).

The junior author reared *A. cingalesa* MOORE successfully on *Pyracantha* species during winter in Germany, and details of the larval instars plus cocoons and living adults are shown here (figs. 57-67). The resulting cocoons were quite different from those of *A. paphia* (L.), with very short peduncles, much smaller size and different surface structure. Due to zoogeographical reasons in combination with morphological differences, *A. cingalesa* MOORE should be viewed with the status of a distinct species.

To complete the survey of these three taxa, we figure small series of ♂ and ♀ specimens of all of them, plus ♂ genitalia, and life cycles, and, in addition, the result of DNA barcoding of selected 40 specimens of *Antheraea* in a neighbour joining tree, with outgroups *Antheraea* (*Telea*) and *Antheraea* (*Antheraeopsis*), plus mainly samples of the subgenus *Antheraea* (*Antheraea*). Also here the separate standing of *A. paphia* (L.) compared to *A. frithi* MOORE can be found, and *A. cingalesa* MOORE is shown to be congenetic in the small analyzed sequence. As argued above, *A. cingalesa* MOORE can be separated from *A. paphia* (L.) using morphological and zoogeographical data.

Conclusion: Some notes on the type material and handling within early taxonomic literature are presented, and we

offer solutions to fix the correct and logical identity of the taxon *A. paphia* (L.) for future taxonomic and biological work. We have presented what we believe to be a compelling case that the name *A. mylitta* (DRURY) is a junior subjective synonym of *A. paphia* (L.), and therefore it should not be used in publications. We have further provided comprehensive assessments of published and new evidence for and against the hypothesis that *A. paphia* (L.) was derived from *A. frithi* MOORE through sericultural activities by humans.

Genetic and genomic studies in recent years have aimed to provide insight on exactly which area of China that sericulture began, and how long ago, by comparing DNA of populations of *B. mori* (L.) and *B. mandarina* (MOORE) from several geographical sources. Comparable studies using nuclear DNA of *A. frithi* MOORE and *A. paphia* (L.) from various localities could possibly answer the same questions of how long ago and where tasar sericulture began, and if *A. frithi* MOORE is indeed the ancestral species of *A. paphia* (L.) and *A. cingalesa* MOORE. So far these questions have not been resolved (nor are they likely to ever be) by comparing pinned specimens in collections, rearing and comparing larvae from several regions, and sampling mitochondrial DNA. We hope that this paper will encourage entomologists or molecular biologists in India to sequence some nuclear genes, or better still, analyze the genomics of these moths to provide additional insights.

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UPSZTY 2007 *Antheraea paphia* (Linnaeus, 1758)
ex. coll. M.L.U.

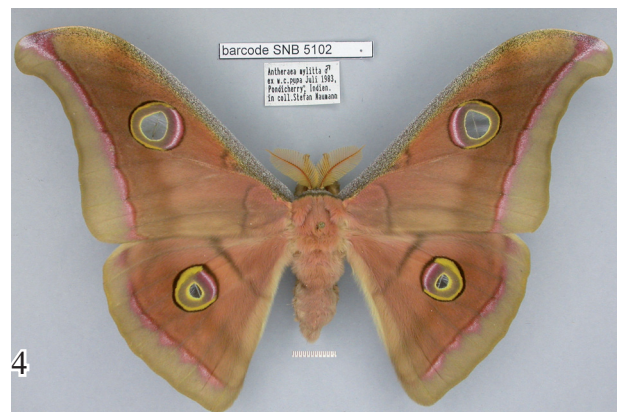
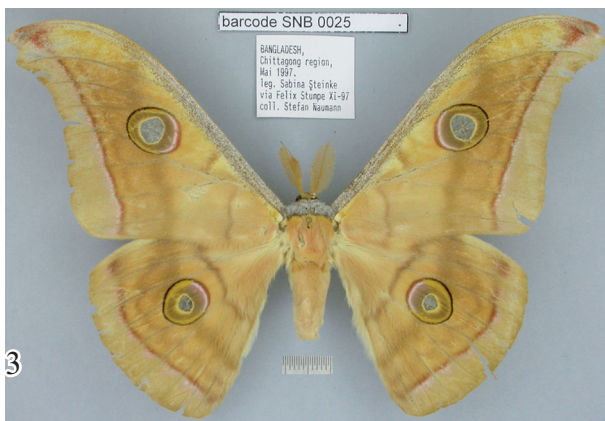
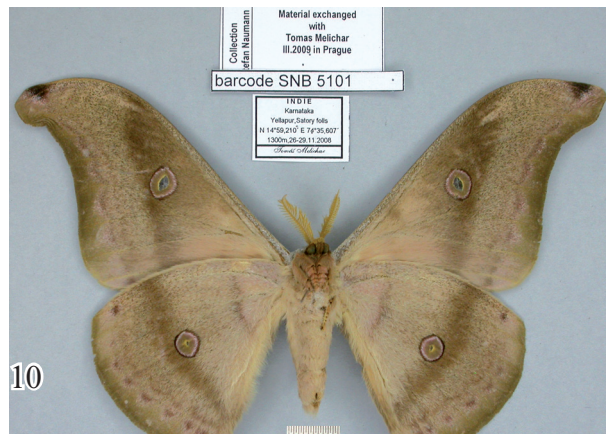
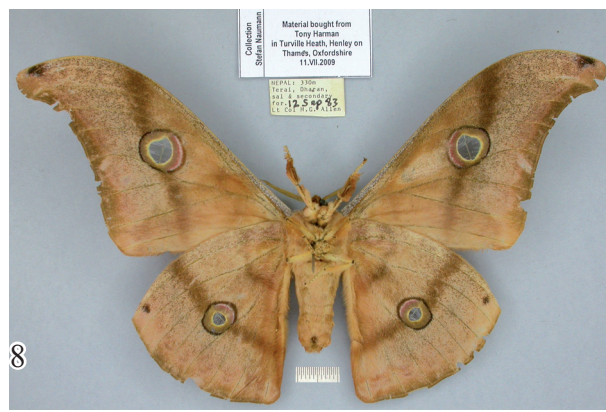
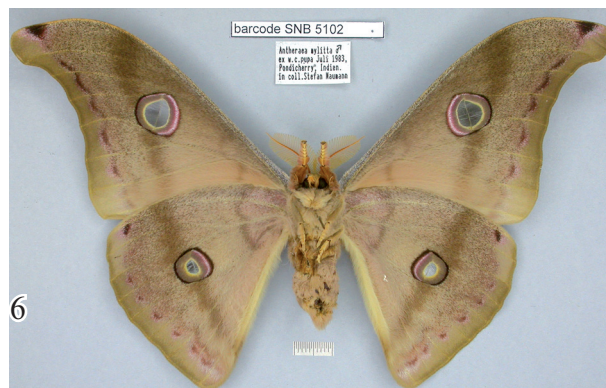


Fig. 1: Only preserved type specimen of *Phalaena Bombyx Paphia* LINNAEUS, 1758 (MLU Uppsala), dorsal view.
Fig. 2: Same specimen as in fig. 1, ventral view plus labels (photo credit: H. MEJLON).
Fig. 3: *Antheraea paphia* (LINNAEUS, 1758), ♂, dorsal view, Bangladesh.
Fig. 4: *Antheraea paphia* (LINNAEUS, 1758), ♂, dorsal view, S. India.



Figs. 5-12: Specimens of *Antheraea paphia* (LINNAEUS, 1758).

Fig. 5: ♂, ventral view, Bangladesh.

Fig. 6: ♂, ventral view, S. India.

Fig. 7, 8: ♂, dorsal and ventral view, Nepal.

Fig. 9, 10: ♂, dorsal and ventral view, SW India.

Fig. 11, 12: ♀, dorsal and ventral view, S. India.

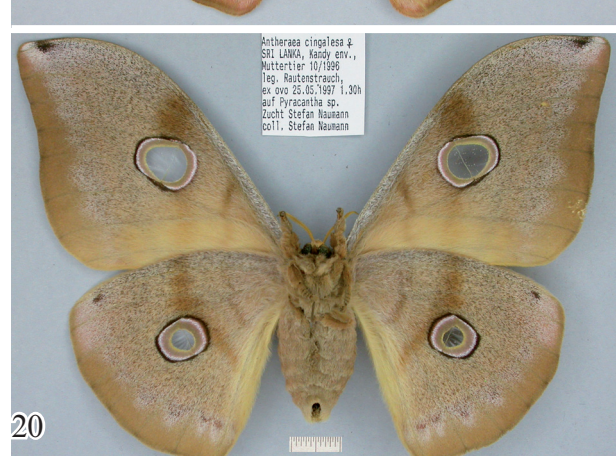
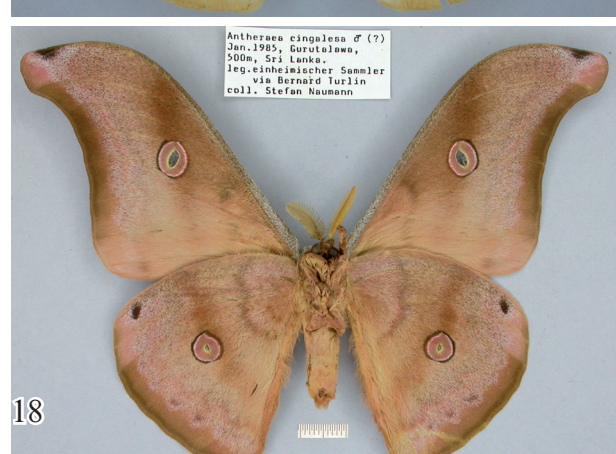
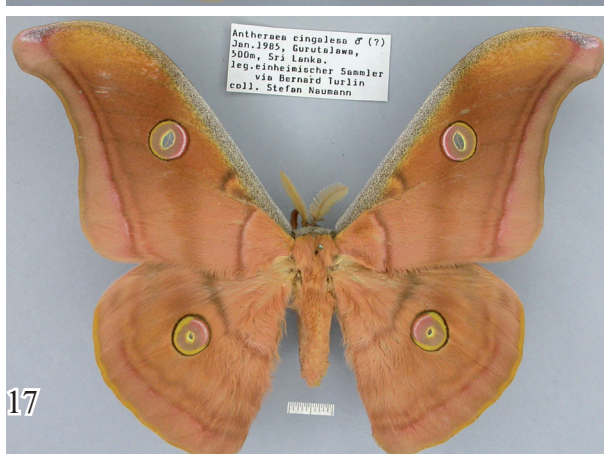
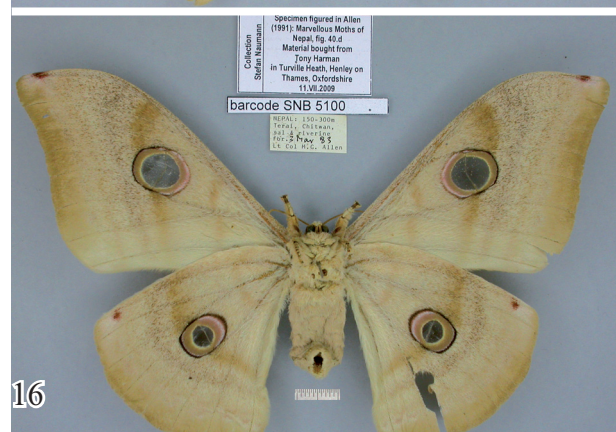
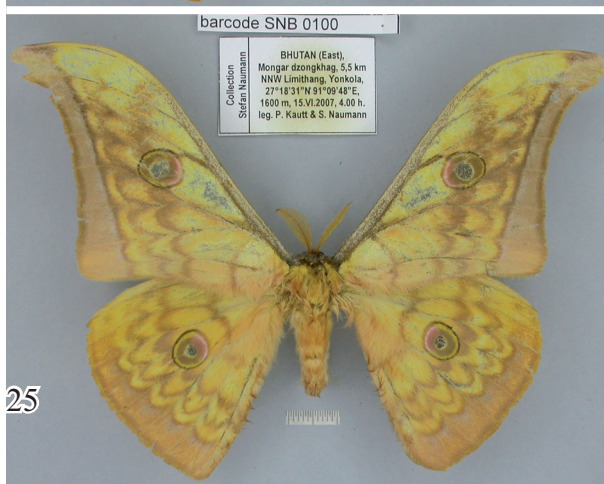
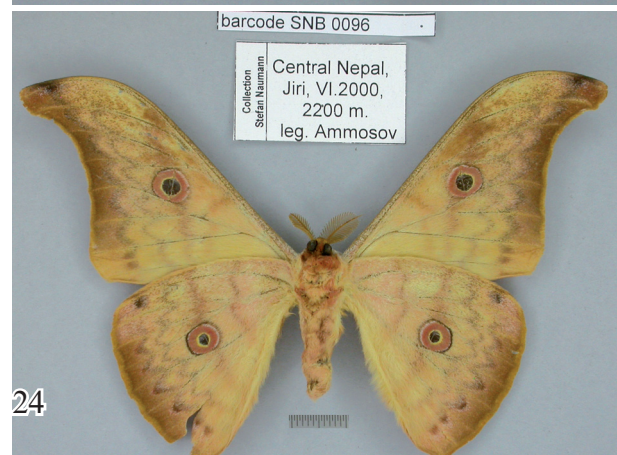
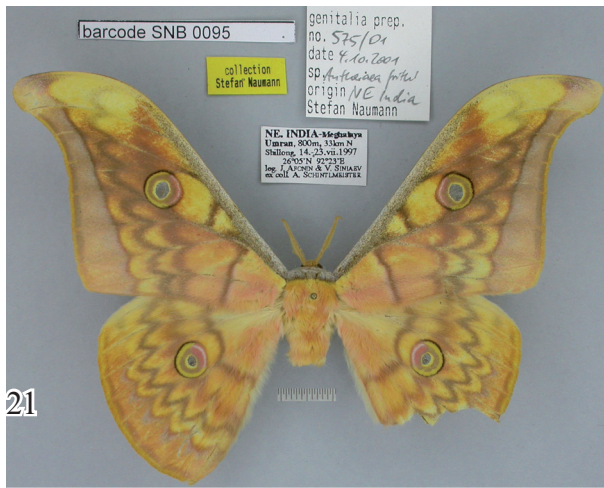
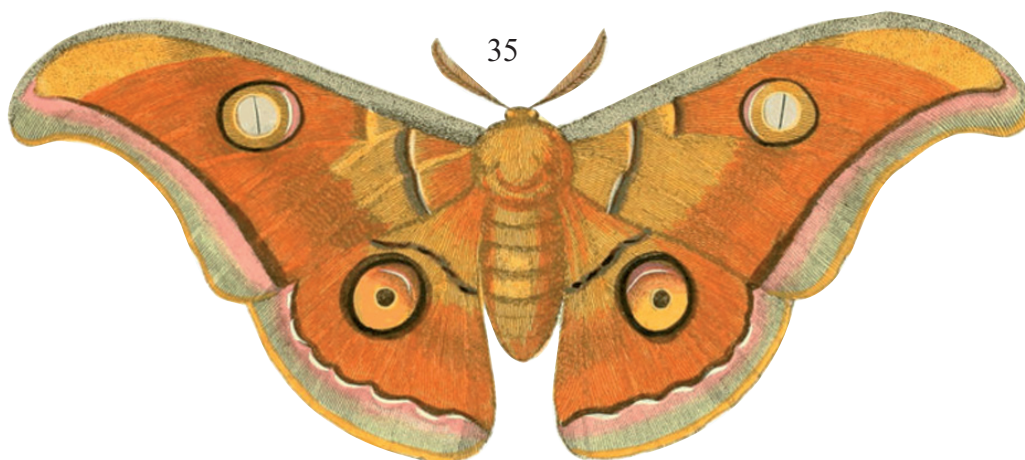


Fig. 13, 14: *Antheraea paphia* (LINNAEUS, 1758), ♀, dorsal and ventral view, Bangladesh.
 Fig. 15, 16: *Antheraea paphia* (LINNAEUS, 1758), ♀, dorsal and ventral view, Nepal.
 Fig. 17, 18: *Antheraea cingalesa* MOORE, 1883, ♂, dorsal and ventral view, Sri Lanka.
 Fig. 19, 20: *Antheraea cingalesa* MOORE, 1883, ♀, dorsal and ventral view, Sri Lanka.



Figs. 21-28: Specimens of *Antheraea frithi* MOORE, 1859.

Fig. 21, 22: ♂, dorsal and ventral view, NE India. Fig. 23, 24: ♂, dorsal and ventral view, Nepal. Fig. 25, 26: ♂, dorsal and ventral view, Bhutan. Fig. 27, 28: ♂, dorsal and ventral view, Tibet.



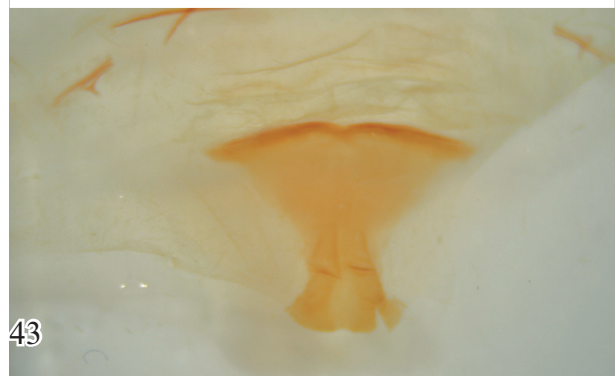
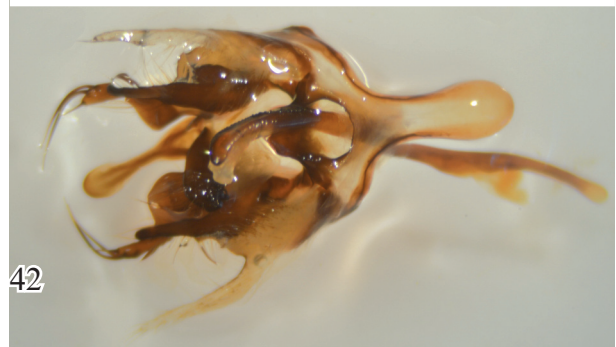
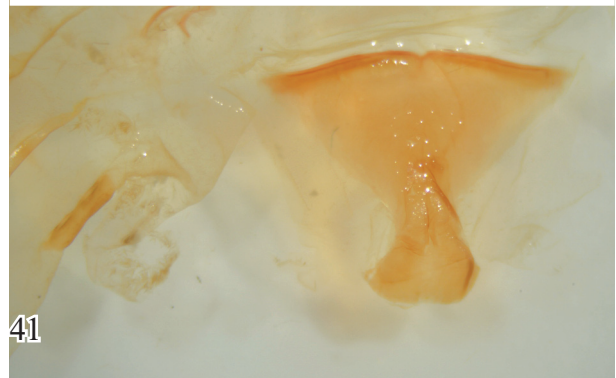
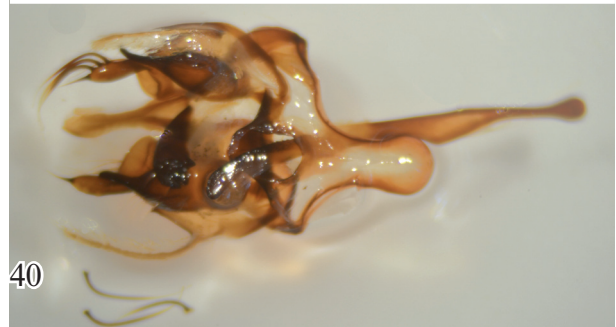
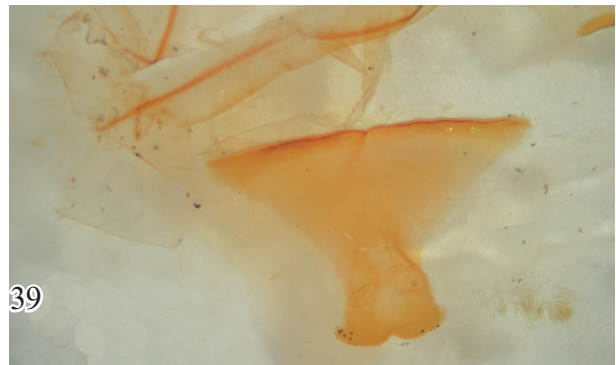
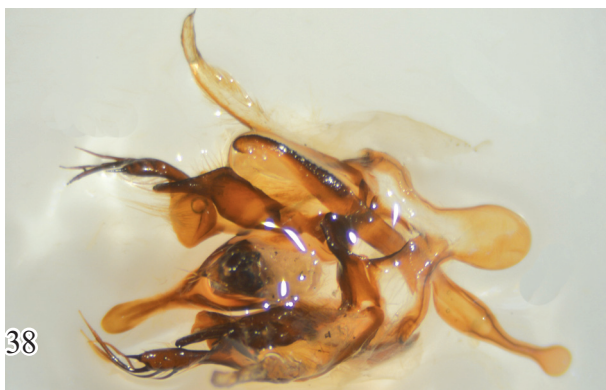
Figs 29-34: Specimens of *Antheraea frithi* MOORE, 1859.

Fig. 29, 30: ♂ dorsal and lateral view, C. Myanmar.

Fig. 31, 32: ♀, dorsal and lateral view, Bhutan.

Fig. 33, 34: ♀, dorsal and lateral view, Tibet.

Fig. 35: Reproduction of the figure of *Antheraea mylitta* (DRURY, 1773), ♂ [figured in DRURY (1773)].

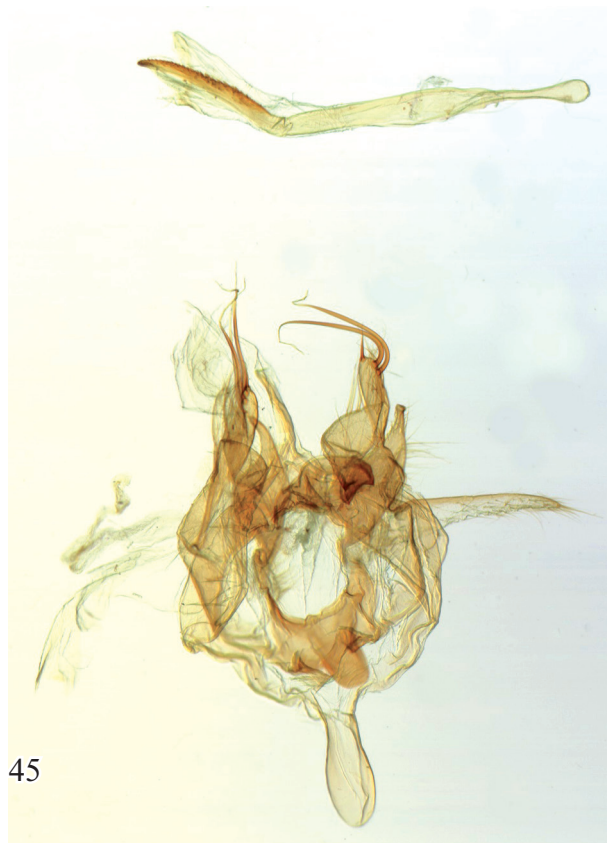


Figs. 36-43: ♂ genitalia structures of *Antheraea* specimens.
 Fig. 36: *Antheraea paphia* (LINNAEUS, 1758), India, prep. no. CBH 0023 (photo credit: U. BROSCHE).
 Fig. 37: *Antheraea paphia* (LINNAEUS, 1758), India, prep. no. CBH 0026 (photo credit: U. BROSCHE).
 Figs. 38, 39: *Antheraea paphia* (LINNAEUS, 1758), SW India, prep. no. 2516/16 SNB, tergum separate.
 Fig. 40, 41: *Antheraea cingalesa* MOORE, 1883, Sri Lanka, prep. no. 2517/16 SNB, tergum separate.
 Figs. 42, 43: *Antheraea cingalesa* MOORE, 1883, Sri Lanka, prep. no. 2518/16 SNB, tergum separate.

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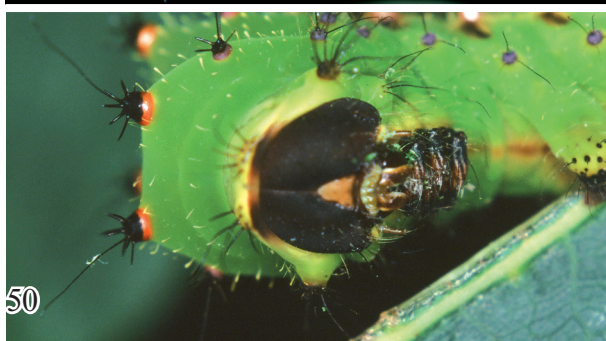


Figs. 44-46: ♂ genitalia structures of *Antheraea frithi* MOORE, 1859.

Fig. 44: Nepal, prep. no. 520/01 SNB.

Fig. 45: Nepal, prep. no. 570/01 SNB.

Fig. 46: N. Myanmar, prep. no. 532/01 SNB.



Figs. 47-56: Early instars and living ♀ of *Antheraea paphia* (LINNAEUS, 1758), India.

Figs. 47, 48: 3rd instar larvae.

Figs. 49, 50: 4th instar larvae.

Figs. 51-54: 5th instar larvae (fig. 52: photo credit: K. WOLFE).

Fig. 55: cocoons.

Fig. 56: ♀, freshly hatched, on its cocoon (photo credit: R. WICKER).



Figs. 57-66: Early instars and living ♂ of *Antheraea cingalesa* MOORE, 1883, Sri Lanka.

Fig. 57: 2nd instar.

Figs. 58, 59: 3rd instar.

Figs. 60, 61: 4th instar.

Figs. 62, 63: 5th instar. Figs. 64, 65: Cocoons and pupa. Fig. 66: freshly hatched ♂ on its cocoon.



Fig. 67: *Antheraea cingalesa* MOORE, 1883, Sri Lanka, freshly hatched ♀ on its cocoon.
 Figs. 68-76: Early instars of *Antheraea frithi* MOORE, 1859, Bhutan.
 Figs. 68-70: 1st instar. Figs. 71, 72: 2nd instar; Figs. 73, 74: 3rd instar. Fig. 75: 4th instar.
 Fig. 76: 5th instar. (Figs. 68 & 76: photo credit: U. WERITZ).



Fig. 77: *Antheraea friithi* MOORE, 1859, Bhutan, cocoon. Fig. 78: *Antheraea friithi* MOORE, 1859, Laos, cocoons. Figs. 79, 80: Four dupattas (shawls) handwoven in India containing natural coloured tasar silk. Fig. 79 (left): From Gujarat with sindhi taropa embroidery and mirrors. Fig. 79 (right): From Odisha with ikat weave in lotus motifs. Fig. 80 (left): From West Bengal with kantha embroidery. Fig. 80 (right): From Kotpad, Odisha, with interlocking temple motifs and red dye from *Morinda citrifolia*. Photos from figs. 79 & 80 by R. PEIGLER, all others (where no photo credit is mentioned) by S. NAUMANN.